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# The Deep History of Earth's Biomass

Sean McMahon<sup>1\*</sup> & John Parnell<sup>2</sup>

<sup>1</sup>*UK Centre for Astrobiology, School of Physics and Astronomy  
University of Edinburgh EH9 3FD, UK*

<sup>2</sup>*School of Geosciences, University of Aberdeen, Aberdeen AB24 3UE, UK*

\* Corresponding email: sean.mcmahon@ed.ac.uk

**Abstract:** The subsurface “deep biosphere” represents one-tenth to one-third of Earth’s total global present-day biomass. The rest is dominated by land plants, a relatively recent development in geological history. Before ~400 Ma, a relatively low surface biomass with high productivity and fast turnover supplied carbon to a deep biosphere with high biomass but low productivity and slow turnover. Here, we argue that the deep biosphere outweighed the surface biosphere by about one order of magnitude for at least half of the history of life on Earth. This result offers a new perspective on the history of life on Earth with important implications for the search for life on other worlds.

Since the realization that life is widespread within the Earth’s crust (e.g. Whitman *et al.* 1998, Heberling *et al.* 2010, Edwards *et al.* 2012), the deep biosphere has been recognized as an ancient, disparate and diverse ecosystem of global biogeochemical significance that provides analogues for habitats on Mars (Fisk & Giovannoni 1999, Weiss *et al.* 2000, Michalski *et al.* 2013) as well as extrasolar planets (McMahon *et al.* 2013). However, estimates of the magnitude of the subsurface biomass on Earth have ranged widely. A highly cited estimate by Whitman *et al.* (1998) proposes a sub-seafloor prokaryotic biomass an order of magnitude greater than the surface prokaryotic biomass, and a sub-continental biomass intermediate between the two. Taking account of land plants, the total subsurface biomass (carbon) would be nearly half of the total global biomass (Whitman *et al.*, 1998); other estimates vary between less than 1% and a third of the total biomass (Fry *et al.*, 2008; Schrenk *et al.*, 2010, Kallmeyer *et al.* 2012; McMahon and Parnell, 2014; Bar-On *et al.*, 2018).

Regardless of which value for subsurface biomass is adopted, it is overwhelmingly dwarfed by ~500 Pg C of land plants (Whitman *et al.*, 1998; Polis, 1999; Saugier *et al.* 2001; Carvalhais *et al.* 2014; 1 Pg = 10<sup>15</sup> g carbon); animals contain less than 2 Pg C (Smil, 2002; Jennings *et al.*, 2008). The high plant biomass reflects colonisation of the free space above the soil, the large mass possible for a rooted sessile organism, access to abundant solar energy, and the preponderance of carbon-rich structural polymers and dead tissues in these organisms. Land plants are a young component of the biosphere, appearing in the Ordovician (~470 Ma) but probably dominating global biomass only since the Devonian-Carboniferous (~380-300 Ma) (Kenrick *et al.*, 2012).

In contrast, the deep biosphere is ancient. Its fossil record is regrettably under-explored, but dates back at least to the early Palaeoproterozoic (Bengtson et al., 2017) and possibly to the Archean (Rasmussen, 2000). The modern deep biosphere is dominated by prokaryotic phyla with evolutionary origins in the Archean, (e.g., *Proteobacteria*, *Firmicutes*, *Chloroflexi*, *Crenarchaeota*, *Euryarchaeota* and *Thaumarchaeota*; Magnabosco et al., 2014, 2016; Parkes et al., 2014; Kieft, 2016; for divergence time estimates see, e.g., Battistuzzi et al., 2004; Magnabosco et al., 2018; Wolfe and Fournier, 2018) and by similarly ancient autotrophic and heterotrophic metabolic strategies, including methanogenesis and sulphur cycling (e.g., Ueno et al., 2006; Shen et al., 2009; Bontognali et al., 2012; Knoll et al., 2016).

These considerations suggest that the deep biosphere could have hosted most of Earth's biomass prior to the Devonian. To investigate this hypothesis, this contribution reviews the distribution of biomass on the modern Earth, and compares it with the interval between ~2.0 Ga and the spread of land plants about 0.4 Ga. This geologically well-documented timeframe post-dates the great oxygenation event at ~2.4 Ga, and represents about half the history of life on Earth.

## **The distribution of biomass**

We revisit the exhaustive classification of Earth's biomass given by Whitman *et al.* (1998) to describe Earth's biomass distribution today and in the interval from 2.0–0.4 Ga, prior to the proliferation of land plants (**Figure 1**).

### **Land plant biomass**

Whitman *et al.* (1998), following Olson *et al.* (1983), estimated total modern plant biomass to be ~560 Pg C, including 470 Pg in forests/woodlands and 90 Pg in other ecosystems. More recent estimates of forest/woodland biomass range from 429 to 536 Pg (Carvalhais *et al.* 2014; Saugier *et al.* 2001). This value can be scaled up to correct for recent deforestation (Crowther *et al.* 2015), yielding a total pre-human plant biomass of ~980 Pg C. Somewhat higher values may have obtained in Earth's history (e.g., during the Carboniferous), but the negative feedback effect of increased forest fires under higher atmospheric oxygen concentrations would not allow global plant biomass to rise much further (Lenton and Watson, 2000).

### **Soil and shallow terrestrial biomass**

*Today:* Soils contain an immense reservoir of organic carbon, but this is mostly non-living detritus (Trumbore, 1997). Whitman *et al.*'s (1998) estimated microbial biomass of 26 Pg in modern terrestrial soils has recently been revised down to ~15 Pg, including all prokaryotes and fungi at the Earth's land surface and within the metre below it (Serna-Chavez *et al.*, 2013).

*Pre-vegetation:* From the Archean until the rise of land plants, the land surface hosted widespread microbial communities reliant on oxygenic photosynthesis for carbon fixation (Konhauser and Lalonde, 2015; Lenton and Daines, 2017). Evidence for these early terrestrial mats and soil crusts includes widely reported geochemical signatures of oxidative weathering, carbon fixation, organic acids and ligand production in palaeosols (e.g., Watanabe et al., 2000; Beukes et al., 2002; Neaman et al., 2005; Crowe et al., 2013; Lenton and Daines, 2017); fossils of terrestrial stromatolites and microbial mats (e.g., Buick, 1992; Eriksson et al., 2000; Prave,

2002); and the rising abundance of sulphur in marine sediments from ~2.5 Ga, attributed to microbial pyrite oxidation on land (Stüeken et al., 2012). It has been suggested that cryptogamic ground cover expanded significantly in the Neoproterozoic, but this is contested (Knauth and Kennedy, 2009; Lenton and Daines 2017).

Plants significantly increase the carbon content, nutrient availability and microbial activity of soil, as well as its volume. However, Serna-Chavez *et al.* (2013) show that soils in tropical forests (the most microbe-rich major soil biome) typically contain only ~4.5x as much microbial biomass per volume as those in arid deserts, the most plant- and microbe-poor land-surface biome. If this sparse desert biome covered the entire ice-free land surface, microbial soil biomass would still be as high as ~5 Pg C. Even in deserts, however, soil microbial biomass is tightly concentrated around plants, and would be much lower without their fertilizing effects (e.g., Gallardo and Schlesinger, 1992; Wardle, 1992; Herman et al., 1995). We therefore suggest a pre-vegetation soil biomass range of ~0.5–5 Pg C.

#### Aquatic biomass

*Today:* Aquatic biomass is dominated by microscopic marine plankton and relatively low in aggregate. Whitman *et al.* (1998) estimated that prokaryotes in aquatic environments represent 2.2 Pg C. Buitenhuis *et al.* (2013) estimated a range of 2.5 to 7.0 Pg C for most marine plankton; including the autotrophic dinoflagellates and some nanophytoplankton missing from this estimate would raise the total to ~3 to 8.5 Pg C (E. Buitenhuis, personal communication).

*Pre-vegetation:* Aquatic biomass reflects a complicated interplay of climatic, bathymetric, biotic and biogeochemical factors. These factors include the nature of the dominant primary producers (once cyanobacteria, now eukaryotes), the supply of nutrients to the photic zone by runoff and upwelling, and the area and volume of shallow seas. It is unclear to what extent the proliferation of land plants increased the delivery of terrigenous nutrients to the oceans; vegetation inaugurated new and more pervasive processes of mineral weathering on land, but also permanently reduced atmospheric CO<sub>2</sub> (suppressing weathering) and increased the retention of fines in terrestrial settings (Algeo et al., 1995; McMahon & Davies, 2018). Nevertheless, the fossil record hints at a gradual increase in marine productivity through the Phanerozoic (e.g., Bambach, 1993; Martin *et al.*, 1996; Falkowski et al., 2004). Primary productivity would have been favoured by higher CO<sub>2</sub> before the Devonian, but suppressed during periods of ocean stratification and redox-controlled phosphorus limitation during the Proterozoic (e.g., Reinhard et al., 2017). Autotrophic aquatic biomass may have been smaller before eukaryotic phytoplankton rose to dominance (Falkowski et al., 2004), and heterotrophic aquatic biomass (today twice as large as autotrophic biomass) would have been much smaller prior to the stepwise oxygenation of the oceans and the rise of metazoans through the Phanerozoic (e.g., Bambach, 1993; Martin *et al.*, 1996). In the absence of better constraints, we suggest that the sum of modern prokaryotic aquatic biomass represents a reasonable first order estimate of total aquatic biomass in the interval from 2.0 to 0.4 Ga; i.e., about ~1.5–3.5 Pg C (Buitenhuis et al., 2013).

#### Subseafloor biomass

*Today:* This reservoir encompasses biomass in sediments and rocks beneath the seafloor. Kallmeyer *et al.* (2012) show on the basis of a large data set that marine sediments support a

biomass in the range of 1.5 to 22 Pg C (expected value  $\sim 4.1$  Pg C), much less than the 303 Pg C proposed by Whitman *et al.* (1998). This dramatic downsizing was upheld by the meta-analysis of Bar-on *et al.*, (2018), which yielded an expected value of  $\sim 7$  Pg C. This biomass is sustained chiefly by heterotrophy, as shown by the fact that cell counts in marine sediments are much higher at continental margins than under the open ocean where very little carbon is buried (Kallmeyer *et al.*, 2012). In contrast, the underlying basaltic/gabbroic basement of the oceanic crust appears to be a significant habitat for chemoautotrophs fuelled by water-rock reactions (Orcutt *et al.*, 2011). Heberling *et al.* (2010) estimated that this largely unexplored region could support a biomass of 200 Pg, chiefly in pillow basalt. However, the few cell counts thus far reported from oceanic basement are much lower than this model would predict, including those measured close to mid-ocean ridges where hydrothermal circulation should create favourable conditions for life (e.g., Mason *et al.*, 2010; Salas *et al.*, 2015 ). The available cell counts have recently been extrapolated to a biomass of oceanic basement in the range 0.5–5.0 Pg C (Bar-On *et al.*, 2018). Total subseafloor biomass today is therefore likely to be close to 10 Pg C.

*Pre-vegetation:* Despite secular continental growth, the volume of the subseafloor habitat has been relatively stable through the last 2 Ga (Heberling *et al.* (2010). The productivity of the sediment-hosted biome is controlled by the burial of organic carbon, most of which derives from marine plankton rather than terrestrial plants. Export productivity may have increased through geological time (e.g., Bambach, 1993; Martin *et al.*, 1996), but productivity is not the sole determinant of carbon burial, and organic-rich shales are common even in the Archean and early Proterozoic (Condie *et al.* 2001; Lyons *et al.*, 2014 ). Indeed, persistent oceanic anoxia until the middle Palaeozoic facilitated copious carbon burial and could at times have supported higher subseafloor biomass than today, especially when shallow seas were more widespread.

Where carbon is plentiful, suitable electron acceptors such as sulphate and nitrate are limiting instead. Subseafloor biomass must have grown both in the basement and the sediment cover as oxidants became increasingly available beneath the oceans—a secular change that began in the Archean and accelerated with the rise of land plants (e.g., Wallace *et al.*, 2017; Stolper & Keller, 2018). The magnitude and rate of the growth in biomass accompanying this gradual shift in redox conditions is difficult to estimate. Energy limitation thresholds are very low in the metabolically ultra-slow deep biosphere (Hoehler & Jørgensen, 2013), methanogens would probably have thrived beneath the low-sulphate Proterozoic oceans (e.g., Habicht *et al.*, 2002; Crowe *et al.*, 2011), and there is plausible fossil evidence of a deep marine biosphere as early as 2.4 Ga (Bengtson *et al.*, 2017). Reconstructing deep subseafloor biomass through deep time is a formidable challenge, but a conservative representative value for  $\sim 2.0$ – $0.4$  Ga would be in the range 5–10 Pg C.

#### Continental deep biomass

*Today:* In contrast to the downsizing of subseafloor biomass, new cell count data from the past two decades have broadly maintained Whitman *et al.*'s (1998) estimate of deep continental biomass in the range of 22–215 Pg C. McMahon and Parnell (2014) derived a range of 14 to 135 Pg from these new data, but taking account of more recent groundwater distribution models (Gleeson *et al.*, 2016) would raise this range to within 10% of Whitman *et al.*'s original estimate. The order-of-magnitude uncertainty remaining stems from the difficulty of scaling up from unattached cell numbers measured in water to total cell numbers that include a majority adhering

to mineral surfaces. However, independent estimates based on pore occupancy models and cell counts from bulk rock/sediment yield ranges of similar magnitude (Whitman *et al.*, 1998; Onstott *et al.*, 1998).

*Pre-vegetation:* Whereas photosynthetic organic carbon supply appears to exert an overwhelming influence on cell counts in marine sediments, no such single overriding factor has been identified in the continental crust, which sustains a higher microbial population density (Kallmeyer *et al.*, 2012; McMahon and Parnell, 2014). The factors limiting continental deep biomass are highly localised, and include photosynthetic carbon supply, electron donors, electron acceptors, and physical conditions, notably temperature (e.g., Moser *et al.*, 2005; Onstott *et al.* 2014); the relative importance of these factors in shaping the total biomass remains unclear.

Carbon limitation was probably more widespread prior to the rise of land plants; cryptogamic ground cover contributes only around ~4% of terrestrial net primary production today (Elbert *et al.*, 2012). However, these communities are highly photosynthetically active; a cm-thick microbial mat can be as productive as a water column tens to hundreds of metres deep (Lalonde and Konhauser, 2015). Moreover, prior to the spread of land plants, these communities would have occupied a much larger proportion of Earth's surface and fixed carbon at a higher rate under the higher atmospheric CO<sub>2</sub> concentrations then prevailing (e.g., Rothschild and Mancinelli, 1990). Microbial mats may also have exported carbon more efficiently to groundwater prior to the development of thick, extensively grazed, organic-rich soil layers, which recycle and respire carbon. Abiotic hydrocarbons, CO<sub>2</sub> and CH<sub>4</sub> would have provided an additional, independent carbon source for the deep biosphere, just as they do today (e.g., Chapelle *et al.*, 2002; Sherwood Lollar, 2007). Molecular hydrogen is also widely available as an alternative electron donor in continental crust (Chapelle *et al.*, 2002; Lin *et al.*, 2005; Sherwood Lollar *et al.*, 2007) and has been generated by radiolysis, serpentinization, and other processes throughout Earth history. Electron acceptors derived from photosynthetic oxygen pervaded the continental subsurface much earlier than the marine subsurface; the sulphate flux from oxidative pyrite weathering was comparable to modern values by 2.0 Ga (Stüeken *et al.*, 2012).

Variation in physical conditions such as crustal thickness, geothermal gradients, and porosity–depth relationships may also have mediated continental biomass through deep time. The balance between sedimentary rocks and crystalline basement in the composition of the continents is especially pertinent, since sedimentary rocks are more porous; today they host ~15× more groundwater—and correspondingly more biomass—than crystalline rocks (Gleeson *et al.*, 2016). Through the Phanerozoic the proportion of basement covered by sedimentary rock fluctuated by a factor of ~2 (Ronov 1980). Erosion which led to the global unconformity at the Precambrian–Cambrian boundary left a paucity of sediment at that time, and has removed much of the Proterozoic record (Peters & Husson 2017). Nevertheless the record of shallow marine sedimentation was constant through the Proterozoic (Peters & Husson 2017) and there is no reason to think that continental composition or total volume in the Proterozoic was systematically different from the Phanerozoic. Taken together, these considerations strongly suggest that the terrestrial subsurface biomass has been, conservatively, at least 10% its current size for ~ 2 billion years, i.e., at least 2–20 Pg C.

## **Discussion**

<b>Table 1.</b>	<b>Continental subsurface</b>	<b>Subseafloor</b>	<b>Aquatic</b>	<b>Soil</b>	<b>Plants</b>
Biomass, Pg C					
<b>With plants (pre-human)</b>	20–200 <sup>a,b,c</sup>	10 <sup>c,d</sup>	3–8.5 <sup>e</sup>	15 <sup>f</sup>	980 <sup>g,h,i</sup>
<b>Before plants (&lt;2.0 Ga)</b>	2–20*	5–10	1.5–3.5	0.5–5	0

\*Conservative lower limit (10% of modern)

(a) Whitman et al., 1998

(b) McMahon & Parnell, 2014

(c) Bar-On et al., 2018

(d) Kallmeyer et al., 2012

(e) Buitenhuis et al., 2013

(f) Serna-Chavez et al., 2013

(g) Saugier et al., 2001

(h) Carvalhais et al., 2014

(i) Crowther et al., 2015

**Table 1.** Illustrative values and approximate ranges of biomass carbon in different reservoirs. Modern (pre-human) values are used for the post-vegetation interval. The pre-vegetation values were estimated by the present study, as explained in the text.

The estimates discussed in the previous section are summarized in **Table 1**. Despite poor constraints on the estimated values of individual biomass reservoirs, it is difficult to avoid the conclusion that subsurface environments hosted the majority of Earth’s biomass from 2.0 to 0.4 Ga. Even if the continental deep biosphere was as little as 10% of its present size (as in **Table 1** and **Figure 1**), the ranges and representative values we derive indicate a deep biosphere carbon reservoir ~1–15× as large as the remaining “surface biosphere” during this interval. Only after the rise of land plants did the biosphere become top-heavy, dominated by eukaryotes, and close to its present size.

Although much of the deep biosphere derives carbon from photosynthesis at the surface, this relationship does not require high surface biomass, only high surface productivity. Marine phytoplankton may account for about half of all primary productivity but contribute less than 1% of global biomass (Falkowski *et al.*, 2004). Similarly, microbial mats and lithic crusts maintain a low standing biomass but rapidly turn over carbon (Lalonde and Konhauser, 2015). Thus, like modern oceans, the ancient continents were probably characterised by high-productivity, low-biomass surface populations and low-productivity, high-biomass deep populations with long carbon residence times.

The extensive evidence for a subsurface biosphere on Earth has raised the possibility that other planets may also support life in a subsurface biosphere (Sherwood Lollar *et al.*, 2007, Edwards *et al.*, 2012). Given that plants proliferated so recently and are expected to die out with declining CO<sub>2</sub> less than 1 Ga from now (O’Malley James *et al.*, 2013), the evidence summarised here suggests that a smaller biosphere dominated by subsurface life could be considered more typical for even the most “Earth-like” inhabited terrestrial planets than the status quo on Earth itself. In fact, the hydrogen-generating mechanisms that occur in the Earth’s crust should all occur on any rocky planet. The constraints of surface water, surface irradiation spectrum and surface temperature used to characterize planetary habitability do not apply to a subsurface biosphere.

Therefore, the number of habitable planets around other stars may be substantially greater than is commonly supposed on the basis of surface habitability (McMahon *et al.*, 2013). Despite the limits of restricted space, there are diverse eukaryotes in the terrestrial deep biosphere, including fungi, nematodes and protists (Ekendahl *et al.*, 2003; Borgonie *et al.*, 2011). Clearly, energy and nutrient availability in the subsurface are sufficient to support complex multicellular life. If life can originate in the subsurface, as implied by some models of abiogenesis (Sleep and Bird, 2007; Martin *et al.*, 2008), a large proportion of life-bearing planets may be inhabited only in the subsurface. Whether such biospheres can ever be detected remains to be seen.

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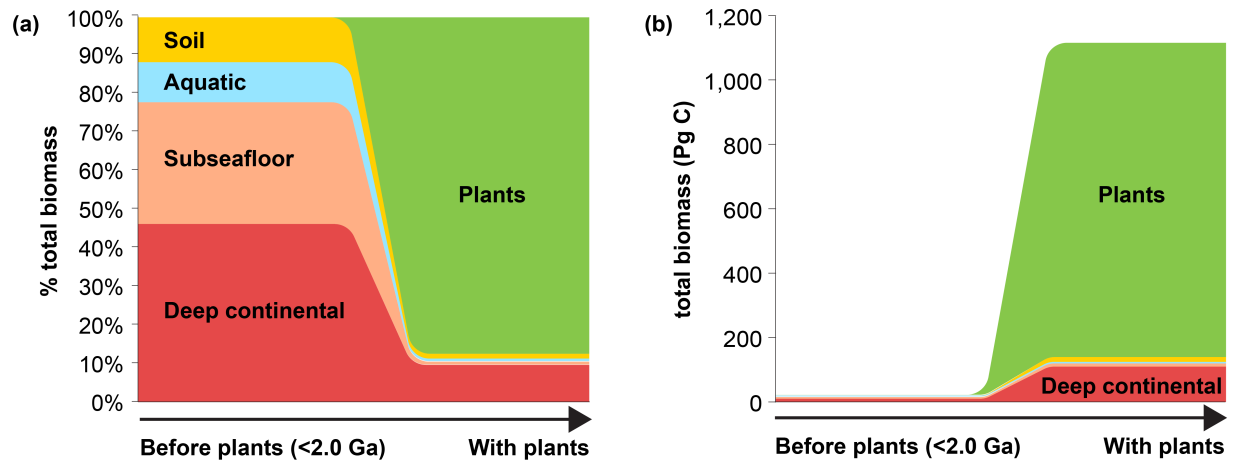
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**Figure 1**



**Figure 1.** Earth's biomass carbon in different reservoirs pre- and post-vegetation, based on the values (and mid-values of ranges) shown in Table 1, (a) as percentages of the total, and (b) as absolute values.